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THE RANK OF NECTURUS AMONG TAILED BATRACHIA.¹

B. F. KINGSBURY.

During the years 1901-1903, I had the opportunity of examining in the Anatomisches Institut of Freiburg i/B., a large number of series through the head of *Necturus*, *Spelerpes* (larval and adult) and *Desmognathus* (larval and adult). I was immediately struck by the very close resemblance between the larval *Spelerpes* and *Necturus*, and drew up the following table, which it seems to me possesses sufficient value to warrant its publication with brief comments. I have rendered it more complete by including in the comparison other forms which must necessarily be considered in this connection, *i. e.*, Axolotl, Siren, Typhlomolge. *Proteus* of course agrees with *Necturus* in all essential points. In addition to information gained from specimens, I have made use of the papers of Wiedersheim,² Parker,³ Cope⁴ and Stejneger.⁵ Especially valuable will be further information as to the cranial characters of *Typhlomolge*. Further work on the cranial anatomy of Siren and the Axolotl would also be important for such a comparison as the following.

Many, perhaps most of the facts presented below are already known but I think their significance is not sufficiently recognized.

¹ I shall use the term "Urodele" and "Urodela," as synonymous with "tailed Amphibian" in this paper, although I realize that such a usage is not quite correct.

² 77. Wiedersheim, R., "Das Kopfskelet der Urodelen," *Morph. Jahrb.*, Bd. III., pp. 352-548.

³ 77. Parker, W. K., "On the Structure and Development of the Skull in the Urodela Amphibia," Pt. I., *Philos. Trans. Roy. Soc.*, Vol. 167, Pt. 2.

⁴ 82a. *Ibid.*, "On the Structure and Development of the Skull in the Urodeles," *Trans. Zool. Soc. London*, Vol. XI., pp. 171-214.

⁵ 82b. *Ibid.*, "On the Morphology of the Skull in the Amphibia Urodela," *Trans. Linn. Soc.*, Ser. 2, Vol. II.

⁴ Cope, E. D., "The Batrachia of North America," *Bull. U. S. Nat'l. Museum* No. 34, 1889.

⁵ Stejneger, L., "Description of a New Genus and Species of Blind Tailed Batrachian from the Subterranean Waters of Texas," *Proc. U. S. Nat'l. Museum*, Vol. XXVIII.

A COMPARISON OF CERTAIN CRANIAL CHARACTERS IN NECTURUS, LARVAL AND ADULT SPELERPES, AMBLYSTOMA AND THE AXOLOTL, SIREN, AND TYPHLOMOLGE.¹

Character.	<i>Necturus.</i>	<i>Larval Spelerpes.</i>	<i>Adult Spelerpes.</i>	<i>Amblystoma.</i>	<i>Axolotl.</i>	<i>Siren.</i>	<i>Typhlomolge.</i>
Frontals,	Present.	Present.	Present.	Present.	Present.	Present.	
Parietals,							
Squamosals,	Present.	Present.	Fused with Pal.-pter.	Fused with Pal.-pter.	Present.	Present.	
Premaxillaries,	Absent.	Absent.	Present.	Present.	Absent.	Absent, ² but bones close.	
Paraphenoids.							
Vomer.							
Vomeropalatine.	See Pal.-pter.	See Pal.-pter.	Fused with Vomer.	Fused with Vomer.	Present.	Present.	
Palatine.							
Pterygo-palatine.	Present.	Present.	Absent.	Absent.	Pal. pter.	Present.	
Pterygoid.	See Pal.-pter.	See Pal.-pter.	Absent.	Present.	Present?	Absent.	
Quadrate and bone "X."	Partly ossified.	Partly ossified.	Entirely ossified.	Ossified.	Present?	Absent? ³	
Nasals.	Absent.	Absent.	Present.	Present.	Present, thin.	Present.	
Prefrontals.	Absent.	Absent.	Present.	Present.	Present?	Absent.	
Maxillary.	Absent.	Absent.	Present.	Present.	Rudimentary.	Absent.	
Pterygoid process of quadrate.					Present.	Short.	Absent.
Nasal capsule.	Imperfect, not connected with cranium.	Absent.	Present, complete, connected with cranium.		Extensive.	Well developed.	
Dentare,	Present.	Present.	Present.	Present.	Present.	Present.	
Angular,	Present.	Present.	Present.	Present.	Present.	Present.	
Articulate.	Absent (as such).	Absent (as such).	Present and fused with angular?		Present.		
Opercular (Splenia).	Present.	Present.	Absent.	Absent?	Present.	Present?	
Intermaxillary gland.	Absent.	Absent.	Present.	Present.		Present.	
Muscles and ligaments.	In <i>Necturus</i> and <i>Spelerpes</i> , morphologically the same.		Altered in metamorphosis.				
Nerves of head.	In <i>Necturus</i> and larval <i>Spelerpes</i> , nearly morphologically the same.		Altered slightly in metamorphosis.				

¹ In the above table, the interrogation point indicates that the statement made in the literature needs careful verification at first hand. A "blank" indicates that nothing is known to the writer concerning the point in question.

² Both vomer and palatine are present and close, but they are not coossified. The Pterygoid portion of the original Palato-ptyergoid, seems to be wanting.

³ Since we cannot be sure whether the Mexican Axolotl was the form worked on, or the larva of *Amblystoma tigrinum*, descriptions by Parker and Wiedersheim are unsatisfactory.

⁴ The palatine portion is present, but the pterygoid portion has apparently been absorbed.

The first five bones mentioned in the above table need no comment since they are universally present. Of the other "roof bones" of the Urodele skull, the nasals and prefrontals which are present in the gill-less adults, are completely lacking in *Necturus* and in the larval *Spelerpes*, and seem to be absent in the larvæ of other forms (as *e. g.*, *Diemyctylus*, Parker, 82a, p. 178), or but slightly developed (*Salamandra*, Parker, 82b). Quite characteristic is the occurrence in the larvæ of Urodela of a Pterygo-palatine (or palato-pterygoid) extending from the ventral side of the quadrate cartilage to the roof of the mouth where as the palatine portion, it is typically tooth-bearing. In the adult gill-less forms, the palatine portion becomes separated from the pterygoid portion and fused with the vomer forming a new osseous skeletal unit, the Vomero-palatine. The Pterygoid portion may be absorbed completely, or remain as a distinct bone, the Pterygoid.

The Maxillare is lacking in the larval forms or if present, as it seems to be in advanced *Amblystoma* larvæ and the Axolotl, it is but weakly developed. In all gill-less adult Urodela it is present.

The quadrate in *Necturus* is peculiar. The lower end, which articulates with the mandible is ossified, while the body of the Quadrate and the otic, trabecular and basilar processes remain cartilaginous. Ossification first appears in a bone, which I call here bone "X"¹ upon the upper (dorsal) surface of the quadrate cartilage, slightly before hatching. It appears to be at first entirely distinct from the cartilage. The lower end soon becomes closely applied to the quadrate cartilage and finally fused with it. From this (as a center?) a zone of ossification spreads inside and outside around the lower end of the cartilage, forming a ring of bone. It was interesting to find in the larval *Spelerpes* a precisely similar method of ossification, identical, it seemed, in all respects with that in *Necturus*, save that the primary ossification was more closely associated with the cartilage. In the larva, the ossification does not proceed beyond the stage found in *Necturus*. The bone "x" coössifies at its distal end with the lower end of the quadrate, but proximally is free from it. In the adult *Spelerpes*,

¹ Cf. Kingsbury, B. F. "Columella Auris and Nervus Facialis in the Urodela," *Journ. Comp. Neurol.*, Vol. XIII., No. 4, 1903.

the entire quadrate cartilage, with the exception of the articular surfaces, has become ossified, with the formation of a marrow cavity, and the primary ossification, bone "x," is no longer distinguishable as a distinct structure. In how far this same mode of ossification prevails among Urodela, I cannot say, but I believe from examination of *Amblystoma*, *Amphiuma* and *Desmognathus*, quite generally.

A cartilaginous process of the quadrate is quite generally found in Urodela extending forward toward the antorbital process of the chondrocranium, forming a "pterygoid arch" (?). Its absence in *Necturus* is noteworthy. It is also absent in the larva of *Spelerpes*, and I believe, most larval urodeles, developing at transformation. Examination of the sections strongly suggested that in both larval *Spelerpes* and *Necturus*, it was present in a "pro-cartilaginous" form.

The Nasal capsule in *Necturus* (and *Proteus*) is quite unique, fenestrated, thin, imperfect, without cartilaginous or bony connection with the chondrocranium. In the larval *Spelerpes* it is absent, developing at transformation.

In the lower jaw, there are comparisons of interest. Briefly stated, the mandibles of *Necturus* and of the larval *Spelerpes* are directly comparable. Each consists of three bones, dentare, operculare (spleniale?), and angulare together with Meckel's cartilage. The angulare seems slightly fused with the articular head of Meckel's cartilage in both *Necturus* and the larval *Spelerpes*. It extends back, forming the "angle" of the jaw, and to its caudal end attaches the mandibulo-hyoid ligament. In the adult *Spelerpes* this bone and the head of Meckel's cartilage are coössified, forming one bone, which perhaps should be termed articulo-angulare, though I believe that the ossification proceeds from the angulare and is at first distinct from the cartilage, in a manner entirely comparable with the ossification of the articular end of the quadrate cartilage. The operculare, a bone present in larval and absent (always?) in adult gill-less life, is, interestingly enough, present in *Necturus*. As to its fate in the adult (gill-less), there is at present, I believe, no satisfactory evidence. I do not believe, however, that it becomes fused with the angulare.

The statements of the relation of muscles, ligaments and nerves

can only be given in general, as my notes fail me for details. The nerves especially indicated are the V. and VII., and the muscles, the muscles of the jaw, hyoid, and branchial apparatus. I regret also that the table is incomplete in the important point—the relations of the branchial arches—so that I cannot state definitely whether there is complete correspondence, *i. e.*, whether the relations of the second basibranchial and the three epibranchials, are the same or not in the two forms.

As cranial characters peculiarly associated with the larval state, are to be mentioned:

1. Presence of a pterygo-palatine and absence of a vomeropalatine.
2. The absence of prefrontals (and nasals).
3. The absence of a processus pterygoideus quadrati (cart.).
4. The absence of a maxillare.
5. Presence of an operculare (spleniale).

All of these characters *Necturus* possesses, and in addition, closely resembles the larval *Spelerpes* in (*a*) the state of ossification of the quadrate, (*b*) the ossifications in the mandible, and (*c*) less clearly, in the rudimentary development of the nasal capsule.

Four possible interpretations of the structural characters mentioned above, and the systematic position of *Necturus*, may be made. (*a*) *Necturus* is a permanent larva, (*b*) it is a degenerate form. (*c*) It is a generalized or low form and (*d*) the possibility should also be considered that *Necturus* owes the structural characters of the skull in which it resembles larval urodeles, to the fact that both are living under very similar conditions of environment—that these characters are in some way connected with the branchial respiration and aquatic life of the form, and represent an adaptation, and adjustment to the environment.

In favor of *Necturus* as a permanent larva stand the larval resemblances enumerated above. Circumstantial support for this view is also given by the generally accepted fact that the gilled Axolotl (*Siredon pisciformis*) is a permanent larval form of a species belonging to the genus *Amblystoma*.

The statement in Cope's *Batrachia*, still holds good, I think. No one has accomplished the transformation of the Mexican Axolotl. On the other hand, the larvæ of *Amblystoma tigrinum*

often grow¹ to enormous size, and undoubtedly are sexually mature while still possessing the larval form (Cope, Osborne²), so that the evidence is good that the Axolotl is a permanent larva.

A tendency to superlarvation seems to exist in other families of tailed Amphibia. *Spelerpes* larvæ attain a length of 60 mm. and I believe an age of two or three years before transforming. Small adults are often of smaller size. *Gyrinophilus porphyriticus*, of the same family, attains a length of twelve centimeters before undergoing transformation. The Museum of Cornell University contains such a specimen, together with adults fourteen centimeters long.

Were the interpretation of *Necturus* as a permanent larva to be seriously accepted, there is no existing form to which it could be related. As far as cranial characters go, the Plethodontidæ, (*e. g.*, *Gyrinophilus*) are temptingly adapted for serving as the transformed kinsmen. However, one very important feature, absence of lungs, of course excludes them from consideration.

The evidence that *Necturus* is a degenerate form, seems to me very slight. There is no reason for regarding the absence of prefrontal, nasal, and maxillary as indications of degeneration. The imperfect condition of ossification about the mandibular articulation also does not seem to me to indicate degeneration. The chondrocranium is much "reduced" in extent; the trabeculæ delicate, the basilar plate imperfect, the nasal capsule incomplete — all of which suggests a reduction from the more usual urodele type. But the place of the chondrocranium has been taken by the bony elements of the skull. The parasphenoid surrounds the cephalic end of the notochord, the frontals and parietals come down to the parasphenoids to complete the side walls of the cranial cavity, so that there is formed a very strong firm skull. From one point of view, perhaps, were *Necturus* regarded as a

¹03, Powers, J. H., "The Cause of Acceleration and Retardation in the Metamorphosis of *Amblystoma tigrinum*; A Preliminary Report," *Am. Nat.*, Vol. XXXVII., pp. 385-410. 1903.

²00, Osborn, H. L., "A Remarkable Axolotl from North Dakota," *Am. Nat.*, Vol. XXXIV., pp. 551-562. 1900.

³01, *Ibid.*, "On Some Points in the Anatomy of a Collection of Axolotls from Colorado and a Specimen from Northern Dakota," *Am. Nat.*, Vol. XXXV., pp. 887-897. 1901.

permanent larva, the fact of superlarvation might itself be regarded as an indication of degeneration. The failure to undergo transformation could be interpreted as, in a sense, arrested development — a form of degeneration.

The evidence that *Necturus* is a low form, seems to me quite as tentative in character as that in favor of *Necturus* as a permanent larva. Cope has placed *Necturus* and *Proteus* in an order, the Proteida, as the lowest of the tailed Amphibia, giving as the critical character the presence of an intercalary bone, relating it to the extinct Stegocephali. Examination of series through the skull, however,¹ shows no such bone present. Apparently what was regarded by Cope as an Os intercalare (Epioticum) is the backward extension of the caudal ossification of the ear capsule (opisthotic?). From examination of figures (no specimens of Stegocephali have been seen by me), the intercalary seems to be a dermal bone and not a part of the ossification of the ear capsule. The ossification in this region is peculiar, consisting, in *Necturus* of a cephalic ossification (proötic?), and a caudal (opisthotic?) which perhaps spreads to it from the exoccipital arch. The homology of the ossifications in the ear capsule in Amphibia as elsewhere, I judge to be in a very unsatisfactory state at present, and even though the Os intercalare belonged to the bones of the ear capsule, it would not be of value in determining the rank of *Necturus* until more is known of the mode of ossification in other tailed Amphibia.

So far as the skull is concerned, the real characters which must be considered in placing *Necturus* low among tailed Amphibia, are, I believe, the same as those which, differently interpreted, afford evidence of *Necturus* as a permanent larva, *i. e.*, the absence of prefrontal, maxillary, etc. If we interpret the larval stage as representing in ontogeny a stage through which the species has passed in its development, then larval characters can be regarded as primitive, and *Necturus* as a primitive form. Aside from the general question of "Ontogeny an Epitome of Phylogeny," such an interpretation of the larval stage is not entirely satisfactory; there are some features that suggest that

¹ There were included specimens 16 mm. long up to an individual 20 cm. in length.

it may be an adaptation. Furthermore, the "ancestor of the Amphibia" would not be expected to be a form with a reduction in the number of cranial bones, but rather the reverse.

It would seem to me worth while to compare other parts of the anatomy of *Necturus* with the larval and adult forms of other urodeles, to see whether there too similar larval characters are to be encountered.

What applies to *Necturus* applies to other gill-bearing forms. If *Siredon pisciformis* never transforms and is yet regarded as a permanent larva, there is no good reason known to me why *Necturus* should not be also considered in the same light. Of the other forms *Proteus*, of course, agrees with *Necturus* in all essential characters. *Typhlomolge* will probably resemble these two when its skeletal characters are made known. Mr. Stejneger in his description of the form says that the maxillary bone is absent and that an intercalary seems to be present. Mr. Lucas is working upon the structural features of the skeleton. His results have not been published as yet, I believe, and will be awaited with interest. *Siren* has been regarded by Cope as a larval form by retrograde metamorphosis. It resembles an "ideal larva" in three of the characters given above — absence of a vomero-palatine, absence of prefrontals, absence of a maxillare.

I believe that the characters in the cranium of *Necturus* that are discussed here are those that are also characteristic of the larvæ of many tailed Amphibia, especially so of certain forms (family Plethodontidæ), and that the acceptance of *Necturus* as a permanent larva best explains at present these features.

It is recognized that there are objections to be met. *Necturus* probably can never be made to transform so that proof cannot be furnished. There is no gill-less adult salamander whose larvæ *Necturus* so closely resembles as does *Siredon pisciformis* the *Amblystoma* larva. *Necturus*, *Proteus* and possibly *Typhlomolge* are very closely alike in structural features, are sexually mature, and occur in different parts of the world. One would not expect them to be permanent larvæ.

An attempt to reach a closer decision leads to a study of metamorphosis in the Amphibia.

CORNELL UNIVERSITY, ITHACA, N. Y.,

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